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A review of the life cycles and life-history adaptations of pelagic tunicates to environmental conditions

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Phylogeny, life cycles, and life-history adaptations of pelagic tunicates to temperature and food concentration are reviewed. Using literature data on lifetime egg production and generation time of appendicularians, salps, and doliolids, r_{max}, the maximum rate of lifetime reproductive fitness, is calculated as a common metric of adaptation to environmental conditions. The r_{max} values are high for all three groups, ranging from ~0.1 to 1.9 d^{-1}, so population doubling times range from ~8 h to 1 week. These high values of r_{max} are attributable primarily to short generation times, ranging from 2 to 50 d. Clearly, pelagic tunicates are adapted to event-scale (i.e. days to weeks) rather than seasonal-scale changes in environmental conditions. Although they are not closely related phylogenetically, all three groups have a unique life-history adaptation promoting high lifetime fitness. Appendicularians have late oocyte selection, salps are viviparous, and doliolids possess a polymorphic asexual phase. There has been little research on hermaphroditic appendicularians, on large oceanic salps, and on doliolids generally. Research is needed on factors regulating generation time, on the heritability of life-history traits, and on age- and size-specific rates of mortality.

Keywords: appendicularian, doliolid, evolution, life cycle, life history, salp, tunicate.

Introduction

Zooplankton life histories provide sensitive clues as to how species have evolved in response to the ever-changing environment of Earth. Life-history information is also required for in-depth understanding of the demography and population ecology of species. Wise management of species for biodiversity conservation, non-indigenous species control, and human harvesting depends on identifying the life-history traits that most affect population dynamics (Forbes *et al.*, 2010).

Life-history traits have evolved to maximize reproductive success in variable environments. However, traits are often constrained by phylogenetic levels of organization. We review here the taxonomic lineage and life cycles of pelagic tunicates and examine how their life-history traits respond to environmental conditions, accounting for some measure of the observed spatial and temporal variability in abundance and species diversity. Life-history characteristics of pelagic tunicates have rarely been investigated, and no review has been attempted. For example, in the comprehensive book edited by Bone (1998), there is only a single chapter on the life histories of appendicularians (Fenaux, 1998a), and none on the life histories of salps or doliolids.

The term Tunicata was coined in 1816 by Lamarck, based upon his observation that all tunicates are covered by a cellulose-like polysaccharide called tunicin. The pelagic tunicates consist of two classes within the subphylum Tunicata, the Appendicularia (or Larvacea), and the Thaliacea, which includes the salps, doliolids, and pyrosomids. Pelagic tunicates share many physical and anatomical characteristics. They are all primarily made of acidic mucopolysaccharides, so are highly transparent, with a high water content (~95% of wet weight; Acuña, 2001). Hence, they are among the most buoyant of all zooplankton, with specific gravities only slightly greater than seawater (i.e. 1.024 g ml^{-1} at 22°C; Tsukamoto *et al.*, 2009). They are holoplanktonic and true suspension-feeders, removing a wide size range of particles from the sea using mucous filters with very fine pores. Pelagic tunicates are, with few exceptions, hermaphroditic. Most species live in the open ocean, but a few, including many of the appendicularians, inhabit continental shelf and even coastal waters. The planktonic tunicates are not highly diverse, with ~70 known appendicularian and 75 thaliacean species.

There are three families within the class Appendicularia: the Oikopleuridae, the Fritillariidae, and the Kowalevskiidae. All are solitary (i.e. there are no colonial appendicularians). Perhaps the best known appendicularian is the small-bodied, temperate species *Oikopleura dioica*. This has a typical oikopleurid body plan, with an ovoid trunk containing the internal organs and

paired pharyngeal gill slits, and a muscular tail containing the notochord and dorsal nerve cord (Fenaux, 1998b). Like almost all species of appendicularian, *O. dioica* is contained inside an acellular mucopolysaccharide structure known as the house, which is used to pre-filter and pre-concentrate food particles before ingestion (Flood and Deibel, 1998). All appendicularian species are hermaphroditic except *O. dioica*, in which the sexes are separate (Fenaux, 1963).

There are three orders within the class Thaliacea: the Salpida, the Doliolida, and the Pyrosomida. As little is known of the life history of pyrosomids, we focus here on the salps and doliolids. All thaliaceans have a complex life cycle including a colonial life-history stage. The small-bodied, neritic salp *Thalia democratica* has received the most attention. It has a typical salp life cycle, with obligatory alternation of sexual (blastozooid or aggregate) and asexual (oozooid or solitary) life-history stages or generations. Both stages are essentially hollow, barrel-shaped animals with a large pharyngeal cavity surrounded by circumferential muscle bands (Godeaux *et al.*, 1998). The internal organs are compacted along the posterior ventral surface of the zooid and the pharyngeal gill slits are reduced to a single, central gill bar. The feeding current is driven primarily by continuous, rhythmic contractions of the circumferential muscles, and assisted by the cilia of the pharyngeal gill bar. All species of salp are hermaphroditic and viviparous, with no larval stage.

Doliolids are relatively small, barrel-shaped animals living primarily in neritic and shelf break waters. They have the most complex life cycle of any of the pelagic tunicates, with not only alternation of sexual (gonozooid) and asexual (oozooid) life-history stages, but polymorphism in the buds produced asexually by the oozooids (i.e. asexual phorozooids and trophozooids; Godeaux *et al.*, 1998). Although there is some anatomical variability among these various life stages, they are all essentially hollow, barrel-shaped animals with a large pharyngeal cavity surrounded by circumferential muscle bands. The internal organs are compacted along the posterior ventral surface of the zooid, and the pharyngeal gill slits are expanded to reach across the entire pharyngeal cavity (Godeaux *et al.*, 1998), a major anatomical difference from salps. The feeding current is driven primarily by cilia of the many ostia perforating the pharyngeal gill. All doliolids are hermaphroditic, and the colonies of asexually produced phorozooids and trophozooids form long, linear chains (Godeaux *et al.*, 1998).

Phylogenetic relationships

The tunicates have long been considered the most closely related invertebrates to vertebrate chordates, so have been of interest in the study of the origins and evolution of deuterostomes generally and chordates in particular (Swalla and Smith, 2008). Early in the last century, Garstang (1928) championed the hypothesis that benthic ascidians are ancestral to vertebrates and that appendicularians are essentially ascidian tadpole larvae that evolved by neoteny (Stach and Turbeville, 2002; Stach, 2007). This theory was based upon painstaking observations of adult morphology, embryology, and larval development. Garstang (1928) then proposed that an early appendicularian-like ancestor led to vertebrate chordates. However, the loss or reduction in structures, as well as the entire life-history stages, has occurred often during tunicate evolution (Lacalli, 1999), rendering inference from morphologically based cladistics of the tunicates problematic.

An alternative view pioneered earlier by Seeliger (1885) was that the Appendicularia represent a sister taxon to the other tunicates (Delsuc *et al.*, 2006; Swalla and Smith, 2008). Under this hypothesis, it was reasoned that a planktonic mode of life is primitive, in accord with the fact that the possible sister taxa of the tunicates are free-living too. It was then proposed that both benthic ascidians and vertebrate chordates were derived from an appendicularian-like ancestor. Hence, there are two hypotheses: that of Garstang (1928), in which benthic forms are ancestral, and that of Seeliger (1885), in which planktonic forms are ancestral.

Beginning in the 1990s, the phylogenetic relationship of the tunicates with vertebrate chordates was clarified by molecular genetics. However, tunicates have proven difficult to pin down using genetic tools, primarily because of the high rates of genetic simplification and mutation (Deneoud *et al.*, 2010). The current view is that echinoderms and hemichordates are sister groups (Supplementary Figure S1, group I) and that the chordates are monophyletic (Supplementary Figure S1, group II), but with the tunicates as a sister group to the chordates, not the cephalochordates (Swalla and Smith, 2008). The thaliaceans are all colonial and a sister group to aplousobranch or phlebobranch ascidians, and the solitary appendicularians either have a long branch (old) and are ancestral to all tunicates or a short branch (younger) and are a sister group of stolidobranch and molgulid ascidians. The most recent work employing new sequencing models suggests that the long branch may be an artefact and that the appendicularians and stolidobranch ascidians are indeed sister groups (Tsagkogeorga *et al.*, 2009). In support of this model is the fact that appendicularians are all solitary, as are most stolidobranchs, whereas thaliaceans are all colonial, as are most aplousobranch ascidians. Hence, whereas appendicularians have a simple life cycle with direct development, thaliaceans demonstrate increasing complexity of the life cycle, into the colonial salps with two life-history stages, and the colonial doliolids with six stages as a consequence of polymorphism of the asexual generation. It has recently been shown too that *O. dioica* shares a unique developmental gene rearrangement with molgulid ascidians that is not shared by other ascidian groups (Wu *et al.*, 2011). Therefore, the molecular evidence suggests that the appendicularian branch is likely short (younger) and that the vertebrate ancestor was benthic, in support of Garstang's (1928) hypothesis.

Life cycles

The appendicularian life cycle is relatively simple, with direct development (Supplementary Figure S2). Most species are solitary, protandric hermaphrodites and fertilization is external (Berrill, 1950; Fenaux, 1998a). The small egg (generally <150 μm in diameter, depending on species) hatches into a tadpole-like juvenile stage. The first filtration house is inflated within hours to a day or so of hatching, depending on species and temperature (Troedsson *et al.*, 2002). Development rate is rapid compared with other tunicate groups. The body wall ruptures during egg release, so all appendicularians are semelparous.

The salp life cycle consists of two life-history stages and obligatory alternation of sexually and asexually reproducing generations (Supplementary Figure S3). The oozooid reproduces asexually by budding from a ventral stolon (Berrill, 1950), the buds being released in a few temporally discrete blocks, though all buds are presumably genetic clones. Hence, the asexually reproducing generation of salps is colonial. The stolon has a central endodermal

canal, a nerve tube, lateral muscle bands, and a strand of gonadal tissue (Lacalli, 1999). At some point during their development, the buds, which are now juvenile blastozooids, are released from the stolon and continue developing and growing in a free-living state. They are fertilized shortly after release by older, functionally male blastozooids (Miller and Cosson, 1997). Sperm are broadcast and collected by the blastozooid feeding net. This is assumed to require some type of swarming behaviour, which is likely synchronous throughout a population and regulated by the ambient light regime (Miller and Cosson, 1997). Fertilization is internal. In most salp species, each female blastozooid contains a single egg. Development is direct, and the growing juvenile oozooid remains attached to its parent via a placenta-like organ, so there is no larval stage and salps are viviparous (Berrill, 1950). The single juvenile oozooid is eventually released from the female blastozooid and becomes free-living, completing the life cycle. As the blastozooids produce a single egg and die following sperm release, they are semelparous.

The doliolid life cycle is similar to that of salps, but with polymorphic asexually produced zooids, called trophozooids and phorozooids (Supplementary Figure S4). The mature asexual stage, called the oozooid (or "Old Nurse'"), produces hundreds to a few thousand buds from a rudimentary ventral stolon, just as in the salps (Braconnot, 1970). However, in the doliolids, the buds leave the stolon and migrate along the inner body wall to a dorsal, stolon-like cadophore, where they align in three paired rows. The buds have different developmental fates depending on their position on the dorsal spur. The central double row of buds develops into phorozooids, and the two lateral double rows develop into trophozooids (Braconnot, 1970). The trophozooids are thought to provide nutrition for the entire colony, which includes not only the developing buds, but also the muscular oozooid, which has by this time reabsorbed its internal organs. The phorozooids are attached to the cadophore by a stalk containing from several to >100 buds, which eventually develop into the gonozooid stage, which later reproduces sexually. The phorozooids become released from the stolon and continue to grow free-living. Upon reaching a threshold size, the juvenile gonozooids fall off the ventral peduncle of the phorozooid and continue to grow in a free-living state. The gonozooids are hermaphroditic and fertilization is internal, although it has not been well described. The fertilized eggs hatch into a tailed larval stage, which quickly reabsorbs its tail and metamorphoses into a juvenile oozooid, which will reproduce asexually, completing the life cycle. All doliolids therefore have indirect development and are essentially semelparous, releasing 2–6 eggs over a period of just a few days (Paffenhöfer and Köster, 2011).

Response of life-history traits to environmental conditions

Life-history theory tries to explain how natural selection acts on organisms to achieve optimum reproductive performance. In essence, this is an issue arising from the allocation of finite resources, the solution to which may depend on the interplay of lineage specific (i.e. phylogenetic) constraints and abiotic and biotic environmental forcing (Southwood, 1977; Sibly and Calow, 1986; Charlesworth, 1994; Stearns, 2000). Trade-offs among life-history traits in turn arise from the timing and proportional allocation of limited resources to maintenance, somatic traits, and reproduction (Stearns, 2000). The demographic cost of reproduction (i.e. decreased survival and future reproduction as a function of present reproduction) is a pivotal trade-off around which life histories are thought to evolve (Fisher, 1930; Williams, 1966). Therefore, reproductive trade-offs constrain the life histories of species, both in terms of flexibility in the expression of key life-history traits and their absolute values (Jokela and Mutikainen, 1995; Ernande *et al.*, 2004). Consequently, by preventing the evolution of Darwinian "demons" (individuals that develop and grow rapidly, reproduce continuously, and do not age), trade-offs in life-history traits, through their effects on future reproductive success, are important determinants of the distribution and abundance of species (Bonsall *et al.*, 2004).

Appendicularians exhibit determinate growth and semelparity. Here, the diversion of limited resources from somatic growth and maintenance to one massive episode of sexual reproduction results in death. In semelparous organisms, development time to maturity is closely related to lifespan or generation time (Troedsson *et al.*, 2002). In general, it is advantageous to develop to maturity quickly (i.e. young) so as to reproduce before being killed by a predator or by environmental bad luck. On the other hand, it is advantageous to mature large so as to produce as many propagules as possible. The trade-off, however, is that it takes longer to grow larger, so increasing the risk of dying before reproducing.

The evolution of parity is dominated by a single factor, the number of progeny produced per lifetime (Zeineddine and Jansen, 2009). The type with the best lifetime reproductive success will dominate a population. Semelparous reproduction evolves when the post-reproductive survival of adults is low, or the time between successive clutches is relatively long. Therefore, reproductive effort is maximized in a single event to compensate for the lack of future reproduction (Sibly and Calow, 1986; Iwasa, 2000; Zeineddine and Jansen, 2009). The predictability of the environment from the perspective of the individual organism in this context is especially important (Southwood, 1977). Environmental variability may include the predictability of food stocks, of encounter with predators, or of physical conditions, all of which vary on a broad continuum of space-and time-scales. If a species experiences its environment as being relatively predictable, it will likely have evolved to mature slowly, have a longer life, produce fewer offspring per brood, and be iteroparous. If a species experiences its environment as relatively unpredictable or ephemeral, it will have evolved to grow and develop quickly, reproduce young, produce a large number of offspring per brood, and spawn only once (semelparous). With this in mind, our review on life-history adaptations of pelagic tunicates will focus on plasticity in age and size at maturity, and lifetime fecundity in relation to temperature and food supply.

Semelparous organisms demonstrate two broad classes of reproductive strategy in response to food concentration (Troedsson *et al.*, 2002). Clutch manipulators have a fixed generation time, but produce more eggs at high vs. low food concentrations (Figure 1). Time manipulators produce a fixed number of eggs under all food conditions, but have shorter generation times at high than at low food concentrations (Figure 1). Of course, in nature, species do not mature at a fixed age or size, but along an age–size trajectory conferring optimal lifetime fitness (Stearns and Koella, 1986). These life-history traits are related to lifetime fitness, taken here as the maximum intrinsic rate of natural increase (r_{max}), determined by the simple equality $r_{max} = \ln b/T$, where b is the lifetime egg production and T the development time from fertilization to spawning (i.e. age at

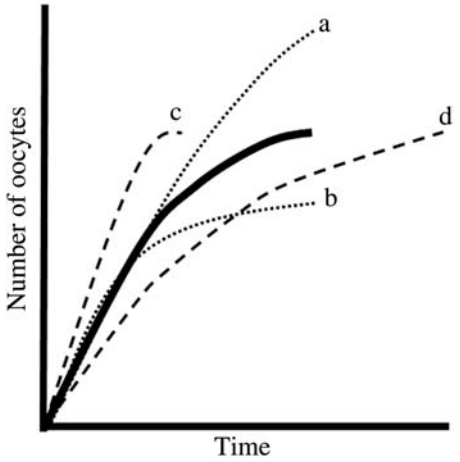

Figure 1. Schematic diagram of different reproductive strategies of semelparous organisms. At one extreme, clutch-size manipulators with a fixed generation time will produce different numbers of oocytes in response to varying nutrient conditions from high (curve "a") to intermediate (bold curve) to low (curve "b"). At the other extreme, time manipulators will produce a fixed clutch size by varying the generation time in response to high (curve "c"), intermediate (bold curve), and low (curve "d") nutrient conditions (adapted from Troedsson *et al.*, 2002).

maturity; Troedsson *et al.*, 2002). As pelagic tunicates are semelparous, T is the generation time. Compared with organisms that exhibit indeterminate growth and iteroparity, the lifetime allocation problem for semelparous organisms without parental care is greatly simplified (Heino and Kaitala, 1999). As can be seen from that equation, T is the most important parameter determining fitness, with the most rapid development rates (i.e. the shortest generation times) favouring greater lifetime reproductive fitness. However, there is a crucial trade-off, rapid development generally meaning smaller body size at maturity, resulting in fewer eggs, and decreasing the numerator of the equation, and lifetime fitness. Hence, the trade-off between age (younger favoured) and size (larger favoured) at maturity is an important determinant of the lifetime fitness of a species. Therefore, growth and development rates are crucial because they have a direct effect on size and age at maturity, two important life-history characters determining reproductive output and lifetime fitness. As the r_{max} parameter encapsulates crucial life-history traits of semelparous organisms, we use it below to compare the response of lifetime fitness of appendicularians, salps, and doliolids to environmental conditions.

Appendicularians

Paffenhöfer (1973, 1975) was among the first to establish *O. dioica* in laboratory culture and utilized this capability to examine the life history of this widely distributed appendicularian. One of his important findings was that generation time was inversely related to temperature, but was constant at food concentrations between 20 and 80 μg C l^{-1}. Gorsky (1980) and Fenaux and Gorsky (1981) confirmed this result for *O. dioica*, which subsequently has been found to hold for many species of appendicularian (López-Urrutia *et al.*, 2003; Lobón *et al.*, 2011; Figure 2a), including *Oikopleura vanhoeffeni*, which may have an annual generation time at −1°C (Choe and Deibel, in press).

The recent experimental and modelling work of Lombard *et al.* (2009a, b) provides a useful synthesis of the relationship among generation time, temperature, and food concentration for *O. dioica* (Figure 2b). We see that generation time decreases rapidly with increasing temperature and increases only slightly with both decreasing and increasing food concentrations outside the optimum range of ca. 80–120 μg C l^{-1}. Hence, generation time at a given temperature is essentially constant across a wide range of food concentration, so *O. dioica* is not a time manipulator in response to increasing concentration of food (Troedsson *et al.*, 2002). This is unusual and is discordant with life-history theory, which predicts declining generation times as food concentration increases (Stearns, 2000). However, it is important to keep in mind that the experiments upon which the model of Lombard *et al.* (2009b) is based were conducted over a food concentration

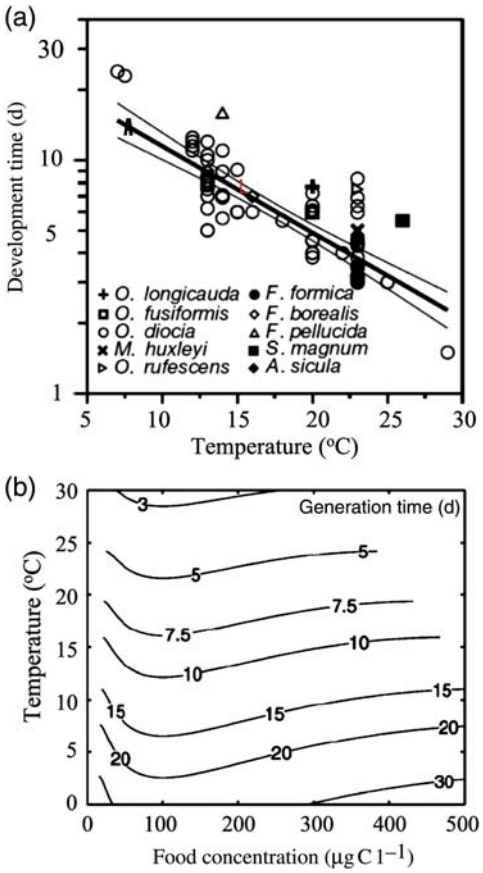

Figure 2. (a) Development time (essentially generation time) of ten species of appendicularian as a function of temperature. The point at L (red) indicates a generation time of 8 d at 15°C for *O. dioica* (Lobón *et al.*, 2011). The lines represent the least-squares linear regression ± 95% confidence limits for parameter estimates. *O.*, *Oikopleura*; *M.*, *Megalocercus*; *F.*, *Fritillaria*; *S.*, *Stegosoma*; and *A.*, *Appendicularia* (adapted from López-Urrutia *et al.*, 2003). (b) Isopleths from a simulation model of generation time as a function of temperature and food concentration for *O. dioica*. Except for food concentrations less than ~80 μg C l^{-1}, generation time at a given temperature is essentially constant with increasing food concentration. The shortest generation times are at the highest temperatures and a food concentration of ~100 μg C l^{-1} (Lombard *et al.*, 2009b, based upon experimental results from Lombard *et al.*, 2009a; reproduced with the permission of Elsevier).

Table 1. Parameters of the lifetime fitness equation[a] for the appendicularian *O. dioica*.

Temperature (°C)	Food concentration (μg C l^{-1})	*b* (eggs individual^{-1} lifetime^{-1})	*T* (d)	r_{max} (d^{-1})	Source[b]	Notes
13	25–80	156	8[c]	0.63	1	Fed I M Cy in the laboratory
		164	8.5[d]	0.60		
		133	8.5	0.58		
		116	10	0.48		
		284	10.5	0.54		
		361	12	0.49		
Mean ± s.d. (*CV*)		202 ± 89 (44%)	9.6 ± 1.4 (15%)	0.55 ± 0.06 (10%)		
12	55	334	11	0.53	2	Fed natural food in the laboratory[e]
12	70–128	304	12	0.48		
7.3	73–80	274	23.5	0.24		
18	ca. 80	41	5	0.74	3	Single families fed I P T in the laboratory
		362	9	0.65		
15	50	64	9.5	0.44	4	Fed I T in the laboratory
	80	89	9.5	0.47		
	100	165	9.5	0.54		
	120	150	9.5	0.53		
Mean ± s.d. (*CV*)		117 ± 48 (41%)		0.49 ± 0.1 (10%)		
25	100	90	5	0.90	5	Model
16		150	7.5	0.67		
12.5		200	10	0.53		
7		400	15	0.40		
Mean ± s.d. (*CV*)		210 ± 134 (64%)	9.4 ± 4.3 (46%)	0.62 ± 0.21 (34%)		
15	100	123 ± 87 (73%)	8.0 ± 2.2 (27%)	0.60[f] ± 0.18 (31%)	6	Half-sibling families fed I Ch in the laboratory

I, *Isochrysis galbana*; M, *Monochrysis lutheri*; Cy, *Cyclotella nana*; P, *Platymonas sueica*; T, *Thalassiosira pseudonana*; Ch, *Chaetoceros calcitrans*. Within each source, rows are in the order of increasing generation time. The sources are arranged in chronological order of publication. Chlorophyll *a* concentration converted to carbon using a factor of 60. s.d., standard deviation; *CV*, coefficient of variation.

[a]Lifetime fitness (r_{max}) = ln b/T, where *b* is the lifetime egg production and *T* the development time, which is equivalent to the generation time in semelparous appendicularians (Troedsson *et al.*, 2002).

[b]1, Paffenhöfer (1973); 2, Paffenhöfer (1975); 3, Fenaux *et al.* (1986); 4, Lombard *et al.* (2009a); 5, Lombard *et al.* (2009b); 6, Lobón *et al.* (2011).

[c]Fed I and M only.

[d]Fed Cy only.

[e]Food concentration based on total chlorophyll *a* concentration (i.e. no pre-filter). Therefore, it is a proxy for the ingestible food concentration, which is unknown.

[f]The only r_{max} value in this table reported in the original publication.

range of 30–120 μg C l^{-1}; model predictions at food concentrations >120 μg C l^{-1} have yet to be verified experimentally. Similarly, the model has been tested experimentally over the temperature range 10–23°C (Lombard *et al.*, 2009b); predictions outside this range may be inaccurate. For example, the published generation times in Table 1 all fall within ≤40% of the predicted values from the model (most are within 20% of the predicted value), except for the single value at a temperature outside the verified range, 23.5 d at 7.3°C (Paffenhöfer, 1975), vs. a prediction of ca. 16 d (Figure 2b).

There is much evidence that decreasing generation time in appendicularians has associated costs. For example, when temperature increases, trunk length at maturity and fecundity generally decrease (Wyatt, 1973; Gorsky, 1980; Fenaux and Gorsky, 1981; Uye and Ichino, 1995; Lombard *et al.*, 2009a). This is so because there is a strong positive relationship between egg production and trunk length (Paffenhöfer, 1973, 1975; Wyatt, 1973; Fenaux and Gorsky, 1981; Lombard *et al.*, 2009a; Figure 3a), which is typical of ectotherms generally (Roff, 2002). Therefore, appendicularians can become reproductively mature and spawn over a wide range of trunk lengths, and larger animals generally produce more eggs, but how might food concentration modulate this effect of temperature on body size at maturity and fecundity? At a fixed temperature, growth rate (plot not shown), size-at-maturity, and fecundity in *O. dioica* all increase with increasing food concentration over the range 20–80 μg C l^{-1} (Lombard *et al.*, 2009b; Figure 3b and c), reflecting the investment of increasing quantities of food in increasing numbers of eggs, which is typical of all appendicularians investigated so far. In fact, well fed, mature *O. dioica* may have from 50 to 70% of their total mass in the gonads (Troedsson *et al.*, 2002; Lombard *et al.*, 2009a). Therefore, generation times are shortest at higher temperatures, but body size and lifetime egg production peak at lower temperatures. How they achieve this increase in the egg production rate in response to increasing food concentration is a valid question.

For semelparous organisms with a short life cycle, such as *O. dioica*, the mechanisms that coordinate the production of mature gametes in concert with favourable environmental conditions are constrained by the short period over which the environment can be sampled by the animal (Troedsson *et al.*, 2002). With a relatively fixed generation time at a given temperature (Figure 2b), the response of *O. dioica* to this challenge is to have evolved the regulation of numerical oocyte production over 2 orders of magnitude, establishing it among the most adept of clutch-size manipulators (Aksnes and Giske, 1990). Just 6 h are required between the initiation of synchronous oocyte growth and the spawning of mature oocytes (Gorsky, 1980; Ganot *et al.*, 2007). During this 6 h period, the previously uniform cytoplasmic content of the ovary (called the coenocyst) is partitioned into

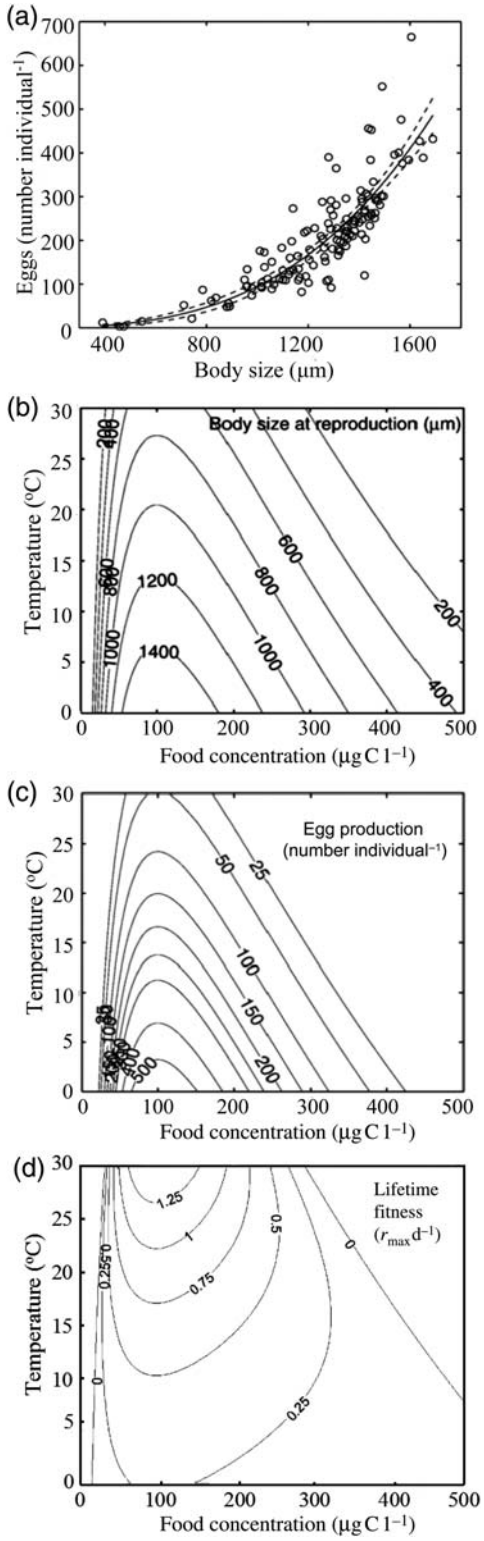

Figure 3. *Oikopleura dioica*. (a) Eggs produced per animal (i.e. lifetime egg production) as a function of body size at a fixed temperature and food concentration (after Lombard *et al.*, 2009a). (b) Isopleths from a simulation model of body size at maturity as a function of temperature and food concentration. Largest body size is at the lowest temperatures and a food concentration of ca. 100 µg C l^{-1}. Body size at maturity decreases as temperature increases and at food concentrations less than and greater than the optimum (after Lombard *et al.*, 2009b). (c) Isopleths from a simulation model of lifetime egg production per animal as a function of temperature and food concentration. Egg production is highest at the lowest temperatures and a food concentration of ca. 100 µg C l^{-1}. Lifetime egg production decreases as temperature increases and at food concentrations less than and greater than the optimum. Egg production increases 20-fold between food concentrations of 40 and 80 µg C l^{-1} (after Lombard *et al.*, 2009b). (d) Isopleths from a simulation model of lifetime reproductive fitness (r_{max}) as a function of temperature and food concentration. Highest lifetime fitness is at the highest temperatures and a food concentration of ca. 100 µg C l^{-1}. Lifetime fitness decreases as temperature decreases and at food concentrations less than and greater than the optimum. Panels (a)–(c) reproduced with the permission of Elsevier; Panel (d) unpublished material courtesy of F. Lombard.

multiple oocytes. In response to unknown triggers, the cytoplasm of the coenocyst and many of the nurse cells is quickly transferred into a subset of selected oocytes. The number of oocytes selected for further development is therefore based on the volume of the coenocyst, which depends on the available food concentration (Ganot *et al.*, 2007). Examination of some hermaphroditic species of appendicularian indicates that this novel mode of oogenesis is a conserved strategy among appendicularians, regardless of reproductive modality (Ganot *et al.*, 2007).

Integration of the above life-history traits into estimates of lifetime reproductive fitness (r_{max}) produces some counter-intuitive results (Table 1). Data from Paffenhöfer (1973, 1975) on *O. dioica* studied in laboratory culture result in an r_{max} range of 0.48–0.63 d^{-1} ($n = 6$, mean 0.55 $\pm$ 0.06). Generation time and r_{max} were much less variable than was fecundity. At slightly lower temperatures with *O. dioica* fed its natural food, Paffenhöfer (1975) obtained data resulting in r_{max} values slightly below that mean, i.e. 0.53 and 0.48 d^{-1} (Table 1). A temperature of 7.3°C is clearly suboptimal for *O. dioica*, because the r_{max} value we calculate from Paffenhöfer's data is just 0.24 d^{-1} (Table 1).

The first evidence of considerable phenotypic plasticity in fecundity and generation time was provided by Fenaux *et al.* (1986), who followed the life cycle of full sibling families from single parent matings at a fixed temperature and food concentration (Table 1). Fecundity varied about ninefold, and generation time ranged from 5 to 9 d. Lifetime fitness is relatively conserved, however, because the increase in fecundity is offset by an increase in generation time, giving r_{max} values of 0.65 and 0.74 d^{-1}.

Because the experiments and model runs of Lombard *et al.* (2009a, b) were conducted over a wider range of food concentration and temperature than the experiments above, the data result in a wider r_{max} range, from 0.40 to 0.90 d^{-1} (Table 1). In experiments run at 15°C and variable food concentration, fecundity and r_{max} both decreased with decreasing food concentration, whereas generation time remained relatively constant. Food concentration <100 µg C l^{-1} seemed to be suboptimal for egg production by *O. dioica*. At a food concentration of 100 µg C l^{-1} and temperatures of 7–25°C, model runs result in a mean r_{max} of 0.62 d^{-1}, similar to previous studies by Fenaux *et al.* (1986) and Paffenhöfer (1973, 1975; Table 1). Again, both the experiments and the model of Lombard *et al.* (2009b) indicate much higher variability of fecundity compared with generation time and lifetime fitness.

Lobón *et al.* (2011) conducted the first controlled breeding experiments using a pelagic tunicate. They investigated the plasticity and heritability of a suite of morphological and life-history characters on several half-sibling families of *O. dioica*. At 15°C and 100 μg C l^{-1} of food, they report fecundity, generation time, and r_{max} values close to those predicted by the model of Lombard *et al.* (2009b) at 16°C (Table 1). Interestingly, they discovered high plasticity of fecundity even among these closely related families, but as is true for other studies of *O. dioica*, much less variability of mean generation time and r_{max}. Importantly, they found that generation time was highly heritable and genetically correlated with r_{max}, whereas fecundity was much less heritable and not genetically correlated with r_{max}. This emphasizes the importance of generation time in setting lifetime fitness and is evidence of a life-history trait that has been strongly constrained by evolution. However, it should be added that although the variability of mean generation time is quite low (*CV* 27%, Table 1), the range in generation time was 4–14 d (Lobón *et al.*, 2011). The frequency distribution of generation time was platykurtic normal, with a low-frequency tail at longer generation times (C. M. Lobón, pers. comm.). Therefore, it would seem that *O. dioica* maintains within its populations an equal and relatively high frequency of short- and medium-length generation time genotypes, and a much smaller frequency of genotypes for long generation times, as insurance against unfavourable environmental conditions.

All studies of *O. dioica* converge on a similar value of r_{max}, between ca. 0.5 and 0.6 d^{-1}. This is similar to the mean r_{max} value of the hermaphroditic appendicularian *Oikopleura longicauda* at 20°C (0.56 d^{-1}; Fenaux and Gorsky, 1983) but somewhat higher than that of the hermaphroditic *Fritillaria pellucida* at 13°C (0.28 d^{-1}; Fenaux, 1976). In general, r_{max} increased with increasing temperature, as a result of a rapid decrease in generation time. This means that the larger animals that took longer to develop generally had lower lifetime fitness than did the smaller ones, although the larger animals produced more eggs. These generalities agree with unpublished r_{max} values from the model of Lombard *et al.* (2009b), showing highest values at temperatures >26°C and food concentrations of ca. 100 μg C l^{-1} (F. Lombard, pers. comm.; Figure 3d). Lobón *et al.* (2011) also found that longer generation times led to much lower lifetime fitness. These are clear examples of the importance of generation time, relative to fecundity, in setting lifetime fitness (Cole, 1954). However, at temperatures >15°C, lifetime fitness at a fixed temperature increases over food concentrations of 20–50 μg C l^{-1} (Figure 3d). This is due to the rapid increase in the rate of egg production at food concentrations of 40–80 μg C l^{-1} (Figure 3c). Hence, appendicularians are clutch-size manipulators (food response) that have evolved to minimize generation time (Troedsson *et al.*, 2002), which is strongly temperature-dependent and heritable (Lobón *et al.*, 2011).

With such short generation times and high values of r_{max}, the question arises as to why dense patches of appendicularians are not common, as is more typical of salps and doliolids. Although little research has been conducted on age- and size-specific mortality in appendicularians, there is an extensive literature of anecdotal reports of various invertebrate and vertebrate predators of appendicularians. Recent mesocosm experiments have shown that appendicularian patches do not form in the presence of normally occurring concentrations of several species of copepod and that copepod predation is heaviest on the eggs and smaller juvenile life-history stages (Stibor *et al.*, 2004). A single estimate of the daily specific rate of mortality of *O. dioica* attributable to copepod predation is ~0.6 d^{-1} (López-Urrutia *et al.*, 2003), essentially equal to the mean values of r_{max} estimated from the literature (Table 1). We conclude that the limited evidence available to date indicates appendicularian populations to be much more strongly regulated by predators than those of salps and doliolids, so high densities of appendicularians may form only when environmental conditions favour short generation times and low levels of predators.

Salps

Salps have direct development (i.e. no larval stage) and release their progeny at a relatively large size (Heron, 1972a; Madin and Purcell, 1992). Viviparity in both sexual and asexual generations

Table 2. Parameters of the lifetime fitness equation for salps[a].

Species	Temperature (°C)	Food concentration (μg C l^{-1})	*b* (eggs generation^{-1})	*T* (d)	r_{max} (d^{-1})	Source[b]	Notes
Thalia democratica	14	?	32	19	0.18	1	Laboratory
			112	20	0.24		
			84	21	0.21		
			72	22.5	0.19		
			56	23	0.18		
Mean ± s.d. (*CV*)			71 ± 30 (42%)	21 ± 1.7 (7.9%)	0.20 ± 0.03 (13%)		
Thalia democratica	22	?	120	2.5	1.9	2–4	Natural food in the field
	16	?	163	14	0.36		
Thalia democratica	20	20–50	54	21	0.19	5	Fed I P in the laboratory
Thalia democratica	20	50	43	2	1.9	6	Natural food in the field
Cyclosalpa bakeri	11	28–49	100	26	0.18	7	Natural food
			170	44	0.12		

Within each source, rows are in the order of increasing generation time. Sources are listed in chronological order. Eggs generation^{-1}, blastozooids produced per oozooid. Chlorophyll *a* concentration converted to carbon using a factor of 60. I, *Isochrysis galbana*; P, *Peridinium trochoideum*; s.d., standard deviation; *CV*, coefficient of variation.

[a]Lifetime fitness (r_{max}) = ln b/T, where b is the lifetime egg production and T the development time, which is equivalent to the generation time in semelparous salps.

[b]1, Braconnot (1963); 2, Heron (1972a, b); 3, Heron and Benham (1984); 4, Heron and Benham (1985); 5, Deibel (1982); 6, Tsuda and Nemoto (1992); 7, Madin and Purcell (1992).

likely reduces the predation losses of progeny, whereas asexual reproduction by strobilation of a large number of buds by the oozooid stage adds considerably to population density with each generation. These factors combine to account for the capacity of salps to form mesoscale patches of animals in a very short period.

Braconnot (1963) was the first to estimate the asexual fecundity and total generation time of a salp. His mean values for the asexual reproductive output of those oozooids that produced buds (i.e. the number of blastozooids produced per oozooid) of 71, and generation time of 21 d for the small neritic salp, *T. democratica*, result in a mean value of r_{max} of 0.20 d^{-1} (Table 2). Similar to the results presented above for *O. dioica*, variability in fecundity was much greater than that of generation time and r_{max}, although the experiments were run at a fixed temperature and controlled, but unspecified, food concentration.

Heron (1972a, b) reported a generation time of just 48 h for *T. democratica*. He determined this value in the field by tracking cohorts during summer at a temperature of 22°C. These generation times remain among the shortest yet reported for a metazoan. However, they may not be sustainable, because a recent field study in the same area demonstrated that such short generation times produced population growth rates that would deplete the water column of all upwelled nitrogen in <1 d (Everett *et al.*, in press).

As do most salps, *T. democratica* produces only a single egg per blastozooid. Therefore, the number of blastozooid buds produced by each oozooid is the only reproductive life-history trait with the plasticity to respond to environmental conditions and upon which natural selection can act. Heron and Benham (1985) determined that the total number of blastozooids released per chain ranged from 25 to 75, depending on oozoid size (Figure 4a). They also found that the number of buds produced per chain varied seasonally, with most produced in winter, when temperature and oozooid growth rates were lowest, and the fewest in spring, when food concentrations and oozooid growth rates were higher (Heron and Benham, 1985; Figure 4b). For estimating the lifetime reproductive output, the number of chains produced per oozooid must also be taken into account, along with data on the number of blastozooid buds produced per chain (see below).

It appears that *T. democratica* overwinters primarily as slowly growing oozoids, producing long chains of blastozooids (Heron and Benham, 1985). The blastozooids are released at relatively low rates and appear to suffer a high frequency of reproductive failure, suggesting density-dependent fertilization success (Heron and Benham, 1985). The oozooids then respond to spring food increases by growing faster and producing fewer blastozooids per chain, but more quickly (i.e. with a shorter generation time). As was the case for *Oikopleura* above, Heron (1972b) concludes that the population growth rate of *T. democratica* is determined primarily by generation time, and not by variability in the number of blastozooid buds released per oozooid.

Estimating lifetime reproductive fitness of *T. democratica* from Heron's work required several assumptions. First, we assumed generation times of 2.5 d for summer and 14 d for winter (Heron and Benham, 1985). Second, we assumed a mean number of blastozooids produced per chain of 48 in summer and 65 in winter (Figure 4b). Third, we assumed that the number of chains produced per oozooid was 2.5, the median of the most commonly observed number of chains (i.e. 2 or 3 chains per oozooid; Heron and Benham, 1985). Therefore, the total number of blastozooids produced per oozooid is 120 in summer and 163 in winter, giving values of r_{max} of 1.9 for summer and 0.36 d^{-1} for winter (Table 2). This is a large range in r_{max}, given the relatively small difference between winter and summer temperatures, which were 16 and 22°C, respectively. Unfortunately, food concentrations were not determined (Heron and Benham, 1984, 1985). As their intrinsic rates of increase are so high, and mortality likely minimal as a result of viviparity (Heron, 1972b), salps tend to overgraze their food resources. Therefore, food supply often limits the salp growth rate and generation time in nature to a greater degree than does temperature (Heron and Benham, 1984).

Deibel (1982) conducted laboratory studies of the asexual fecundity and generation time of *T. democratica* (Table 2). His values for fecundity and generation time led to an r_{max} value of

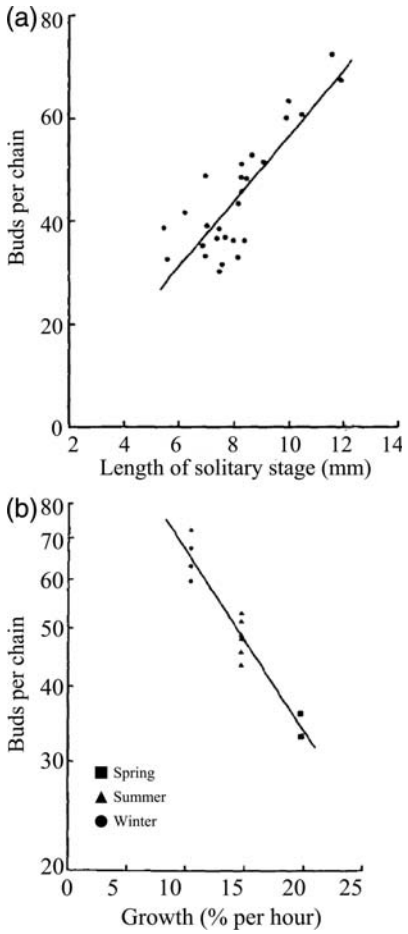

Figure 4. *Thalia democratica*. (a) Number of blastozooid buds produced per chain (or block) as a function of oozooid body size at maturity. As the size at maturity of the oozooids increases, the number of blastozooid buds produced also increases. During its lifetime, an oozooid produces either two or three chains of blastozooids. (b) Number of blastozooid buds produced per chain (or block) as a function of oozooid growth rate and season. Chain size is least in spring and greatest in winter, but oozooid growth rates are greatest in spring and least in winter. Winter and spring water temperatures were almost identical (16 and 16.5°C, respectively). Food concentrations were not determined. Generation time in summer was ca. 2.5 d and in winter ca.14 d. Spring generation time was not reported. Both panels after Heron and Benham (1985) reproduced with the permission of Oxford University Press.

0.19 d^{-1}, a factor of 10 lower than the maximum values of Heron (1972a, b), but close to the values of Braconnot (1963), which were also determined in the laboratory, and within a factor of 2 of Heron's (1972a,b) minimum winter values. In comparison, Tsuda and Nemoto (1992) used a similar cohort-tracking technique to that used by Heron (1972a, b), leading us to estimate an r_{max} value of 1.9 d^{-1} from their data, based on a generation time of just 2 d (Table 2). The disparity between laboratory determinations of r_{max} for *T. democratica* (Braconnot, 1963; Deibel, 1982), and cohort-tracking studies in the field (Heron, 1972a, b; Tsuda and Nemoto, 1992), is likely attributable to assumptions and limitations of both approaches, and it highlights the difficulty in conducting life-history studies of delicate gelatinous zooplankton. The field estimates are based on the assumptions that a single population is being marked and tracked with drogue drifters over several days, that plankton nets collect accurate samples reflecting true salp abundance, and that plankton nets do not cause the loss of blastozooids from the stolon. The laboratory estimates are based on the assumptions that the food particles offered reflect the diet and food concentrations in nature, that the food is maintained in suspension during the experiments, that the animals feed normally, and that confinement in containers does not negatively affect stolon length and hence the number of blastozooids produced. That the field estimates of r_{max} may be too high is supported by the observations of Everett *et al.* (in press; see above) and Tsuda and Nemoto (1992), who indicated that the animals in their patches were grazing nearly the entire primary production of 1 g C m^{-2} d^{-1} each day. However, the laboratory estimates of r_{max} in Deibel (1982) may be too low because the food concentrations offered were lower than is typical during patch formation, and because confinement may have negatively impacted feeding rates and blastozooid production (Heron and Benham, 1984; Madin and Deibel, 1988; Paffenhöfer and Gibson, 1999). There is clearly need for further research into population growth rates and reproductive fitness of salps in both the field and the laboratory before convergent estimates of r_{max} can be derived.

Madin and Purcell (1992) published one of only a few papers on oceanic salps, which are much larger than the neritic *T. democratica*. Working in the NE Pacific on *Cyclosalpa bakeri*, they found that oozooids produced 170 blastozooids over a lifespan of ca. 30 d at 11°C. The blastozooids were 8–10 mm long when released from the stolon and spawned their single embryo ca. 14 d later at a length of ca. 50 mm. The total generation time of 44 d results in an r_{max} value of 0.12 d^{-1} (Table 2). This estimate was based on average growth and development rates in aquaria on board ship. The high-growth-rate model presented by Madin and Purcell (1992) resulted in a generation time of ca. 26 d, from which we estimate an r_{max} value of ca. 0.18 d^{-1} (Table 2). Hence, the lifetime fitness of the large, oceanic *C. bakeri* is less than that of the field estimates for the smaller, neritic *T. democratica*, but similar to the laboratory estimates for *T. democratica*.

Doliolids

There has been much less research on the life histories of doliolids than on appendicularians and salps. Most of the work has focused on the distribution and abundance of doliolids in relation to hydrography and only recently have laboratory studies been undertaken that allow the examination of basic life-history characteristics, such as sexual and asexual fecundity, stage lifespan, and total generation time.

Table 3. Parameters of the lifetime fitness equation[a] for *D. gegenbauri* (Paffenhöfer and Gibson, 1999).

Life stage	Gonozooid	Larva	Oozooid	Phorozooid
Progeny $stage^{-1}$	4 eggs	–	1 400 phorozooids	140 gonozooids
Stage lifespan (d)	12	4	21	15
Cumulative progeny	4	4	5 600	784 000
Cumulative time (d)	12	16	37	52
r_{max} $generation^{-1}$ (d^{-1})	–	–	–	0.26

Stage lifespan, the time for each stage to produce 50% of its progeny. Laboratory experiments were run at 20°C and at a food concentration of 60–90 μg C l^{-1}.
[a]Lifetime fitness (r_{max}) = ln b/T, where b is the lifetime egg production and T the development time, which is equivalent to the generation time in semelparous doliolids.

In the 1960s, observations were made of dramatic but short-lived population outbursts of doliolids in the field. Braconnot (1963) observed that the small coastal doliolid *Doliolum nationalis* often had pronounced abundance peaks in late winter and spring. Working with a 23-year dataset from the same station, Ménard *et al.* (1998) established that doliolid peaks were coincident with stratification of the water column and phytoplankton blooms. These observations led to the hypothesis that *D. nationalis* must be food-limited in the NW Mediterranean Sea.

The field observations of Braconnot (1963) were extended by others in the late 1970s, and an association between cold cores, Gulf Stream spin-off eddies, resultant phytoplankton blooms, and dense, mesoscale patches of *Dolioletta gegenbauri* was documented (Deibel, 1985). Field and companion laboratory observations (Deibel, 1982) suggested that doliolid patches were strongly regulated by environmental conditions, particularly food concentration.

Subsequent laboratory studies unravelled the life-history characteristics underlying these mesoscale blooms. The large (up to 1.2 mm) larva is short-lived, and within 4 d at 20°C, metamorphoses into a young oozooid (Deibel, 1982). At food concentrations of 20–160 μg C l^{-1}, mature oozooids produce ca. 70 phorozooids per day for 20 d, or ca. 1400 phorozooids per oozooid (Paffenhöfer and Gibson, 1999; Table 3). If we assume that the reproductive lifespan of the oozooid stage is equivalent to the time of release of 50% of its progeny (Heron, 1972a), we have an oozooid stage lifespan of ca. 21 d (Table 3).

Within 4 d of being released, the phorozooids begin to release gonozooids from the ventral peduncle (Paffenhöfer and Gibson, 1999). The extent of the reproductive stage of the phorozooids decreases exponentially with increasing food concentration (Gibson and Paffenhöfer, 2002), as predicted by life-history theory, but the lifetime reproductive output peaks between 20 and 60 μg C l^{-1} (Figure 5). Therefore, it appears that food concentration is important in setting both the asexual fecundity and stage lifetime of doliolids. However, much less is known about the asexual reproductive output of the oozooids, and its potential response to food concentration. Gonozooids live for 10–14 d (Paffenhöfer and Köster, 2011), releasing an average of four eggs per gonozooid (Deibel, 1982). Hence, the reproductive output of 784 000 progeny over a generation time of 50 d results in a value of r_{max} of 0.26 d^{-1} (Table 3), giving a population doubling time of ca. 2.5 d.

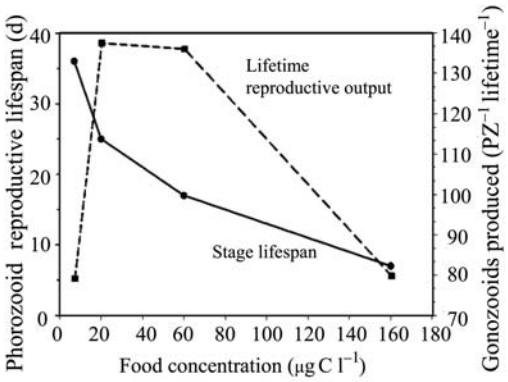

Figure 5. The reproductive lifespan (related to generation time) and lifetime asexual reproductive output of *D. gegenbauri* phorozooids (calculated from the original data), as a function of experimental food concentration. Stage lifespan curve adapted from Gibson and Paffenhöfer (2002).

Food concentration has an effect on some other life-history characteristics of doliolids which may impact bloom-forming ability. When food is limiting, phorozooids opt to release their gonozooids on time rather than on fecundity, i.e. they produce a smaller number of gonozooids at smaller phorozooid body size (Paffenhöfer and Gibson, 1999; Gibson and Paffenhöfer, 2002). However, the size of newly released gonozooids is independent of food concentration (Gibson and Paffenhöfer, 2002). Hence, like appendicularians, doliolids show some of the characteristics of clutch-size manipulators, operating at a generation time fixed primarily by temperature and secondarily by food concentration. Given their complex life histories, it is likely that the ability of doliolids to form swarms is a combination of high rates of asexual reproduction and short generation times. The r_{max} value for doliolids is within the range of those for appendicularians and salps (Tables 1–3), indicating that doliolids overcome their longer generation time with much more asexual fecundity (i.e. 3–4 orders of magnitude higher than salps). Therefore, it seems that doliolids and salps have evolved two different solutions to the same problem. Doliolids have developed greater fecundity (both sexual and asexual) and longer generation times, and salps lower lifetime fecundity, but shorter generation times.

Overview and future research needs

The r_{max} values calculated here from literature data on lifetime fecundity and generation time are high for all three groups, ranging from ca. 0.1 to 1.9 d^{-1}. Therefore, population doubling times range from ca. 8 h to 1 week. These high values of r_{max} are attributable primarily to short generation times, ranging from 2 to 50 d. Clearly, pelagic tunicates are adapted primarily to event-scale (i.e. days to weeks) rather than seasonal-scale environmental variability. Although they are not closely related phylogenetically, all three groups show unique life-history specializations, allowing high lifetime fitness. Appendicularians have direct development, late oocyte selection, and short generation times and are clutch-size manipulators in response to increasing food concentration. Salps also have direct development, but are viviparous and have alternation of sexual and asexual generations. Doliolids also have alternation of sexual and asexual generations, but possess a polymorphic asexual phase, allowing very high reproductive output per generation. Doliolids also seem to have asexual clutch-size manipulation in response to food concentration.

Much research remains to be carried out on life-history adaptations of pelagic tunicates. There has been little research on hermaphroditic appendicularians, on large, oceanic salps, or doliolids generally. Research is especially needed on factors regulating generation time and on the heritability of life-history traits. Ingenuity will be required to obtain accurate and precise estimates of generation time, however, because small differences in this parameter have a large effect on lifetime reproductive fitness. There is very little information on age- and size-specific rates of mortality of pelagic tunicates, but it will be required to extend these life-history observations to estimates of population demography and dynamics.

Supplementary material

Four figures are provided as Supplementary material in the *ICESJMS* online version of this paper, depicting the deuterostome phylogeny of the group, and the life cycles of appendicularians, salps, and doliolids, respectively.

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